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The overview of lithobiomorph centipedes (Chilopoda, Lithobiomorpha) from caves of Slovenia

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Abstract

Centipedes of temperate regions can be found in various habitats, including forest litter, soil or caves. Slovenia, situated in the Northwestern Balkans, has rich centipede fauna, with one of the earliest scientific descriptions of a cave centipede, *Lithobius stygius* Latzel, 1880, from Postojnska jama. Many lithobiomorph species have been reported from Slovenian caves, but the data on their occurrence are scattered in the literature or public collections, and several specimens have even remained unexamined. Here we present the overview of lithobiomorph centipedes found in Slovenian caves. Altogether, 21 lithobiomorph species were found in 160 localities. The majority of the records, 319 out of 410, are published for the first time. Only three species are considered exclusively subterranean species, *L. stygius*, *L. zveri* and *Eupolybothrus obrovensis*, while other species are surface dwellers. The potential explanation of surface species presence in caves is discussed. We comment on cases of unresolved taxonomical status and present suggestions for further research needed to resolve them. Even though lithobiomorph centipedes often occur in caves, their role and importance in subterranean habitats remain to be studied.

Keywords

biodiversity, *Eupolybothrus obrovensis*, Lithobiidae, *Lithobius stygius*, *Lithobius zveri*, subterranean

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Introduction

Centipedes are important predators in various ecosystems, ranging from tropical to subpolar climates (Voigtländer 2011). In temperate regions, where they reach very high species richness, centipedes inhabit various habitats, including forest litter, soil, human buildings and caves, with humidity being the crucial factor influencing their occurrence (Bonato and Zapparoli 2011; Voigtländer 2011). Even though centipedes have regularly been found in caves all over the world, only a small share of them are presumed to be troglobitic (e.g., Edgecombe 2005; Chagas-Jr and Bichuette 2018; Edgecombe et al. 2020; Stojanović et al. 2021). The interest for the centipedes in caves has a rich history where the first subterranean centipedes were described in France (e.g., *Lithobius coquerellii* Lucas, 1860, *Lithobius cavernicolus* Fanzago, 1877 and *Lithobius speluncarum* Fanzago, 1877), but reports on their occurrence date even earlier. In the Balkans, the first described subterranean centipede was *Lithobius stygius* Latzel, 1880 from Postojnska jama, in Slovenia (Latzel 1880). Most of the subterranean species belong to the order Lithobiomorpha, however, some troglobiotic Geophilomorpha and Scolopendromorpha have been described as well, also from the Balkans (Stoev et al. 2015; Shear and Krejca 2019; Vahtera et al. 2020).

With more than 250 species, the Balkan Peninsula is one of the richest regions in the world regarding the centipede species richness (Bonato and Zapparoli 2011; Simaiakis and Strona 2015), of which more than half (142 species) belong to the order Lithobiomorpha (Stoev 1997). At its Northwestern part, in Slovenia, there is relatively high proportion of centipede species richness – between 58 (Bonato et al. 2016) and 86 (Stoev 1997) species are reported in the checklists, around half of them belonging to the order Lithobiomorpha, family Lithobiidae (Kos 1992a; Stoev 1997; Simaiakis and Strona 2015; Bonato et al. 2016). Three lithobiid genera were reported for the country, namely *Lithobius* Leach, 1814, *Harpolithobius* Verhoeff, 1904 and *Eupolybothrus* Verhoeff, 1907.

The knowledge on the centipede diversity on the area of today's Slovenia, including caves, accumulated over time. The first important contributions were by Latzel (1880); Verhoeff (1929, 1930, 1933, 1937b, 1943); Attems (1908, 1929, 1959) and Manfredi (1932b). In the second half of the 20th century, centipedes gathered in caves were studied mostly by Matic (Matic and Dărăbanţu 1968; Matic and Stentzer 1977; Matic 1978, 1979). Their work resulted in the description of three currently valid exclusively subterranean species, *Lithobius stygius* Latzel, 1880, *Lithobius zveri* (Matic & Stenzer, 1977) and *Eupolybothrus obrovensis* (Verhoeff, 1930). More recently, the data on centipedes in caves was gathered sporadically in general overviews of centipedes diversity (e.g. Zapparoli 1989; Kos 1992a) or during cave fauna inventories (e.g. Novak 2005; Polak et al. 2012; Polak and Pipan 2021; Zagmajster et al. 2021). In the last two decades, a lot of new centipede material from caves has been collected as part of different faunistic studies. It mostly remained as grey literature (reports, bachelor thesis), unpublished or even as unexamined material. Furthermore, the data was scattered in various literature sources and several collections and there was no overview of species found in caves of the country.

To fill the gap and present the up-to-date overview of the lithobiomorph centipedes in the caves of Slovenia, we have compiled the available data from published and unpublished sources. Besides giving the overview of the records and the species list, we

present taxonomic challenges regarding the identification of species and recommend the main directions for further studies on this important, yet heavily understudied group.

Materials and methods

Geographical setting

Slovenia, with an area of 20,273 km^2, lies at the junction of four major European geographical macro-regions: the south-eastern part of the Alps, the western margin of the Pannonian Basin, the north-western part of the Dinaric Alps and the northern margin of the Mediterranean (Perko et al. 2020). The country's complex geological history has influenced the development of various landforms, topography, bedrock, soil types, hydrology, climate and vegetation. The climate ranges from sub-Mediterranean to temperate continental and montane (Perko et al. 2020). On average, there is 1750 mm of precipitation annually, which are spatially and temporally highly variable (Komac et al. 2020). The average annual temperature in Slovenia is between 10 and 13 °C (Komac et al. 2020). The primary vegetation in most parts of Slovenia is temperate forest (Andrič and Willis 2003; Šilc et al. 2020), which covered 58% of the country in 2020 (SURS 2021).

An important geographical feature of Slovenia is the karst, special type of landscape, where water soluble carbonate bedrock enables formation of fissures and caves (Gams 2004). There are over 14,000 caves registered in Slovenia, some of which are more than 1000 m deep (Karst Research Institute ZRC SAZU 2022; Ljubljana Cave Exploration Society 2022). Karst areas cover 43% of the country and are divided into three principal areas: Alpine karst, Isolated karst and Dinaric karst (Gams 2004; Zupan Hajna 2004).

Data compilation

Information on the occurrence of lithobiomorph species in caves was taken primarily from the database on subterranean biodiversity SubBioDB (managed by the Subterranean Biology Lab, Department of Biology, Biotechnical Faculty, University of Ljubljana), including data until the end of 2022. SubBioDB combines literature data and the data on individuals collected during various fieldwork expeditions. One record refers to the unique combination species-locality-source for literature data and species-locality-date for new (fieldwork) data.

Specimens reported as new findings were collected in the fieldwork by visual inspections and direct hand picking or, in some cases, by baited pit-fall traps. All individuals were preserved in 70% or 96% ethanol and stored in the Zoological collection of the Subterranean Biology Lab, Department of Biology, Biotechnical Faculty, University of Ljubljana. Some specimens were contributed to this collection from the collections of the Notranjska Museum in Postojna (Slavko Polak), or the speleobiological collection of the Department of Biology, Faculty of Natural Sciences and Mathematics, University of Maribor (Peter Kozel). In addition, some older material was taken from the "Chilobio" centipede collection of the Animal Ecology Group, University of Ljubljana (Ravnjak

and Kos 2015). Specimens were examined under stereomicroscope Olympus SZH10 or Leica M165 C and morphologically determined using identification keys for lithobiomorph centipedes (e.g. Matic 1966; Koren 1992; Stoev et al. 2010). In cases where reliable species identification was not possible, e.g., due to damaged, juvenile or female individuals, specimens were identified only to a genus level.

Species taxonomy followed the one proposed in ChiloBase 2.0 (Bonato et al. 2016). We implemented this also for the already existing literature records, where names were curated to follow currently valid taxonomy. As an exception, *Lithobius jugoslavicus* Matic & Darabantu, 1968 was treated as a synonym of *Lithobius stygius* Latzel, 1880, following the taxonomic status of its substitute name *Lithobius corneliae* Stoev, 1997. Furthermore, *Lithobius punctulatus* was considered a synonym of *Lithobius validus*, following Eason (1972) and Kos (1987). Reassignments of taxa were made in four cases, where reports of species *Eupolybothrus leostygis*, *Eupolybothrus fasciatus*, *Lithobius burzenlandicus wardaranus* and *Lithobius microps* were assigned to *E. obrovensis*, *E. grossipes*, *Lithobius* sp. and *Lithobius carinthiacus*, respectively. The rationale behind these reassignments is explained in the discussion.

Geographic positions of cave entrances were taken from the Cave Registry of Slovenia ("Kataster jam Slovenije"), available at https://www.katasterjam.si/ (Ljubljana Cave Exploration Society 2022), or from GPS coordinates (in cases of caves whose registration is in progress and artificial tunnels). Few localities reported in literature were, due to dubious geographic position, assigned to wider geographic areas or region and not to individual caves. Distributional maps were produced using QGIS, ver. 3.16. (QGIS Development Team 2021).

Data resources

The data underpinning the analysis reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility, and are available at https://www.gbif.org/dataset/2bce5608-b366-4e65-8dbe-6870da7888b2.

Results

Lithobiomorph centipedes were found in 155 subterranean sites (153 caves and two artificial tunnels, Table 1) throughout Slovenia and five less exactly determined subterranean localities (Suppl. material 1). They are reported for the first time from 114 (71%) localities (Fig. 1).

Altogether, 410 occurrence records of lithobiomorph centipedes were gathered, of which 91 (22%) are literature and 319 (78%) new records (Table 1). The records refer to 21 valid species from three genera. Most of the recorded species (18) are known primarily from the surface habitats (Fig. 2), while three of them are considered to be subterranean (Fig. 3).

Table 1. The overview of lithobiomorph centipedes, found in caves of Slovenia. In the column "Literature findings" reports on published records are given, with references and notes on taxa or locality reported in brackets. In the column "New findings", reports on findings that have not been published before are given, with dates, initials of legators and an information whether the animal was found in the part close to the cave entrance (entrance part) or away from the entrance, in the aphotic zone of the cave (deeper part) (when this information was specified in the label). Obligate subterranean species are in cells, shaded in light grey colour. New records come from SubBioDB, with exception of the ones marked with *, that come from ChiloBio dataset. Reported new findings, where the material could not be examined by an expert are marked with #. Coordinates and details on cave positions can be found in the Suppl. material 1. Initials of the legators refer to: AJ – Ana Janović, AK – Anja Kos, Aka – Andrej Kapla, AL – Ana Lozar, AM – Ajda Moškrič, AP – Anja Pekolj, AZ – Aja Zamolo, BR – Behare Rexhepi, BS – Boris Sket, CF – Cene Fišer, DC – David Culver, DK – Darja Kolar, Dku – Džana Kuna, DŠ – David Škufca, EP – Ester Premate, EvP – Eva Pavlovič, FG – Franci Gabrovšek, FK – Franc Kljun, FP – Franc Potočnik, GB – Gregor Bračko, HR – Hans Recknagel, IK – Ivan Kos, JB – Jana Bedek, JJ – Jure Jugovic, JM – Janja Matičič, JS – Janez Stražišar, JZ – J. Zver, KK – Katarina Kanduč, KlK – Klara Kač, LK – Lucija Knauf, LL – Ljerka Lah, LR – Lucija Ramšak, MB – Matej Blatnik, MaP – Matija Perne, MiP – Mitja Prelovšek, MK – Marjeta Konec, MR – Maša Rajh, MS – Marjeta Smrdel, MV – Miloš Vittori, NS – Nataša Sivec, PeP – Petra Pavšič, PG – Primož Gnezda, PK – Peter Kozel, PP – Primož Presetnik, PT – Peter Trontelj, ŠB – Špela Borko, SiP – Simona Prevorčnik, SM – Stefano Mammola, SP – Slavko Polak, TD – Teo Delić, TT – Tjaša Trajbarič, Unk – Unknown, US – Uroš Stepišnik, VS – Valentin Schein, VZ – Valerija Zakšek, ŽF – Žiga Fišer, ŽK – Žan Kuralt, MZ – Maja Zagmajster, UK – Urška Kamenšek.

Taxon name	Literature findings	New findings
Eupolybothrus (*Eupolybothrus*) *grossipes* (C. L. Koch, 1847)	Jama pod južnim vrhom Tisnika (Matic and Stentzer 1977), Jelenska jama (Matic and Dărăbanţu 1968 (as *E. fasciatus*, re-examined in this study)), Razpoka (Matic and Stentzer 1977)	Jama nad Kobilo (10.9.2022, leg. TD), Kadunjška jama (21.6.2014, leg. DŠ, NS), Krivopeta jama (15.5.2022, leg. TD), Mrzla jama pri Ložu (16.7.2007, leg. SP), Predjamski jamski sistem (2.9.2020, leg. PK, deeper part), Rivčja jama (2.8.2021, leg. DŠ, TD, EP)
Eupolybothrus (*Parapolybothrus*) *obrovensis* (Verhoeff, 1930)	Dimnice (Matic and Dărăbanţu 1968; Ozimec and Komerički 2009; Ozimec et al. 2011; Polak et al. 2012 (some references relate to the type locality, given by Verhoeff as "Hohle bei Obrov", Matic and Dărăbanţu (1968) report also on finding from this cave)), Istria (Verhoeff 1933), Medvedjak jama (Attems 1908, 1929 (as *E. leostygis*); Eason 1983; Verhoeff 1933; Wolf 1938 (as *E. obrovensis and E. leostygis*); Polak et al. 2012), Pečina v Borštu (Verhoeff 1930; Wolf 1938 (both relate to the type locality, given by Verhoeff as "Hohle bei Obrov")), Polina peč (Polak et al. 2012)	Jama pod Krogom (26.7.2018, leg. EP), Račiška pečina (27.4.2004, leg. SP), Štefakova pečina (24.5.2020, leg. AK, JS, entrance part), Velika Kozinska jama (12.1.2014, leg. MZ, TD)
Eupolybothrus sp.		Jama pod Smoganico (16.9.2020, leg. AK, entrance part), Lisičji grad (25.7.2018, leg. EP), Polina peč (3.2.2006, leg. SP)

Taxon name	Literature findings	New findings
Eupolybothrus (*Leptopolybothrus*) *tridentinus* (Fanzago, 1874)	Jama za Hudim lazom 1 (Kos 1988), Jerinovec (Matic and Dărăbanţu 1968 (as *E. leptopus*)), Mačkovica (Kos 1988), Planinska jama (Matic and Stentzer 1977 (as *E. leptopus*)), Zadlaška jama (Verhoeff 1929 (as *Polybothrus cerberus*, loc. as Dantegrotte bei Tolmin); Manfredi 1932b (as *Polybothrus cerberus*, loc. as Grotta Dante presso Tolmino); Wolf 1938 (as *Polybothrus cerberus*, loc. as Dantegrotte); Eason 1983 (loc. as Grotta Dante near Tolmin)	Babja jama (22.7.2010, leg. MZ), Babja luknja (21.9.2020, leg. AK), Jama nad Kobilo (10.9.2022, leg. TD; 24.2.2007, leg. BS; 27.10.2009, leg. PT, SiP), Jama pod Gradiščarjevim robom (19.6.2009, leg. MZ, JJ), Jama v Lozi pri Orehku (14.5.2020, leg. AK, JS), Kamrica jama (2.7.2021, leg. MZ, TD, EP), Košelevka (17.12.2021, leg. EP, BR, entrance part; 13.4.2022, leg. CF, EP, deeper part; 20.4.2022, leg. AK, CF, entrance part; 4.5.2022, leg. BR, AL, TT, entrance part; 27.10.2022, leg. MZ, BR, AK, AP, entrance part), Snežna jama pri Glažuti (22.9.2020, leg. AK, MR), Topli vrh 5 (21.2.2021, leg. TD), Velika Knežja jama (17.5.2020, leg. AK, JS), Željnske jame (22.9.2022, leg. AK, MR), Zelške jame (19.6.2022, leg. AK, entrance part)
Harpolithobius gottscheensis Verhoeff, 1937		Košelevka (13.4.2022, leg. CF, EP, entrance part; 10.11.2022, leg. VZ, HR, MZ, entrance part), Topli vrh 5 (21.2.2021, leg. TD), Zavinka jama (26.12.2021, leg. AK, deeper part), Zelške jame (19.6.2022, leg. AK, entrance part)
Lithobiidae	Kubik jama (Polak et al. 2012)	Belojača[#] (10.11.2003, leg. UK; 18.12.2003, leg. UK, record kept under name *Lithobius* sp.), Kozja luknja[#] (record kept under name *Lithobius* cf. *stygius*), Jama Tunel v Spodnji Idriji[#] (27. 10. 2009, leg. MZ, SiP, record kept under name Lithobiomorpha)
Lithobius agilis C.L.Koch, 1847	Babja luknja (Matic and Dărăbanţu 1968), Huda luknja pri Gornjem Doliču (Matic and Stentzer 1977), Jama pod južnim vrhom Tisnika (Novak and Kuštor 1982), Jama pri Votli peči pri Ravnah (Novak and Sivec 1977), Jelenska jama (Matic and Dărăbanţu 1968)), Pilanca (Matic and Stentzer 1977; Novak and Kuštor 1982), Planinska jama (Matic 1979)	Babja luknja (28.3.2006, leg. MiP), Košelevka (17.12.2021, leg. EP, BR, entrance part)
Lithobius austriacus (Verhoeff, 1937)		Artificial tunnel at Osek (23.7.2011, leg. MZ)
Lithobius borealis Meinert, 1868		Jama med plastmi (20.7.2020, leg. AK, JS, entrance part)
Lithobius carinthiacus Koren, 1992	Jelenska jama (Matic and Dărăbanţu 1968 (as *L. microps,* re-examined in this study)), Vratnica (Matic and Dărăbanţu 1968 (as *L. burzenlandicus wardaranus*, tentatively assigned, re-examined in this study))	Apolonova jama (17.5.2020, leg. AK, JS, entrance part), Blažev spodmol (26.7.2018, leg. EP), Gašpinova jama (9.7.2021, leg. AK, entrance part), Jama pri jami pri kalih (18.8.2020, leg. AK, JS, entrance part), Košelevka (12.7.2022, leg. AK, MZ, Dku, deeper part), Lešanov brezen (11.6.2020, leg. MZ, ŠB, TD, entrance part), Merjaščeva jama (14.6.2020, leg. AK, JS, entrance part), Polharjev kevderc (1.9.2020, leg. AK, JS, entrance part), Skednena jama (18.8.2020, leg. AK, JS)
Lithobius castaneus Newport, 1844		Topli vrh 5 (21.2.2021, leg. TD)
Lithobius dentatus C.L. Koch, 1844		Jamovka (13.10.2022, leg. GB, AP, deeper part)
Lithobius erythrocephalus C.L. Koch, 1847	Carniola (Attems 1959), Hrencova jama (Matic and Dărăbanţu 1968), Istria (Attems 1929 (as *Archilithobius illyricus*)), Jama pod Smoganico (Zapparoli 1989), Pivka jama (Zapparoli 1989), Planinska jama (Zapparoli 1989), Podpeška jama (Zapparoli 1989)	
Lithobius forficatus (Linnaeus, 1758)	Postojnska jama (Wolf 1938), Predjamski jamski system (Wolf 1938 (loc. as Luegger hohlen))	Jama v Pruhu (29.7.2011, leg. MZ)
Lithobius latro Meinert, 1872	Koševlevka (Matic and Dărăbanţu 1968)	
Lithobius lucifugus L. Koch, 1862	Golobeja jama (Verhoeff 1937a (as *Lithobius microporus*))	

Taxon name	Literature findings	New findings
Lithobius melanops Newport, 1845	Raja peć (Folkmanová 1946 (as *Lithobius glabratus fuscus*, Lok. 776, Vranja pečina))	
Lithobius nodulipes Latzel, 1880		Brezno pri Pojetovih lazih 2 (2.7.2020, leg. AK, JS, entrance part), Doljna vodena jama (20.7.2019, leg. EP), Hajdučka jama (19.11.2022, leg. EP), Jama jugozahodno od Mašuna (29.9.2002, leg. SP), Jama med plastmi (20.7.2020, leg. AK, JS, entrance part), Jama pod Gavgami (3.6.2022, leg. AK, MZ, entrance part), Jama v Mlaki (21.1.2007, leg. SP), Jezerski kevderc (1.9.2020, leg. AK, JS, entrance part), Koševlevka (21.6.2020, leg. AK, JS, entrance part; 30.3.2022, leg. AK, MZ, TD, entrance part; 5.4.2022, leg. BR, GB, deeper part; 10.11.2022, leg. VZ, HR, MZ, entrance part), Pajkova Reža (27.10.2014, leg. ŠB), Pečina v Borštu (4.9.2022, leg. AK, entrance part), Pistišekova povšna (20.11.2003, leg. Aka), Polharjev kevderc (1.9.2020, leg. AK, JS, entrance part), Skednena jama (18.8.2020, leg. AK, JS), Slugova jama (26.3.2017, leg. MZ), Špehovka (19.7.2016, leg. EP, AJ), Otoška jama (24.10.2003, leg. LR, entrance part), Trpinova jama (22.5.2022, leg. AK), Tunnel at Spodnja Draga (9.7.2014, leg. DŠ), Velika jama nad Trebnjem (28.7.2009, leg. MZ), Velika Kozinska jama (12.1.2014, leg. MZ, TD), Veliki Hubelj (15.1.2015, leg. ŠB), Vidovec (19.11.2022, leg. EP), Viršnica (22.5.2022, leg. AK), Zadlaška jama (21.7.2010, leg. MZ)
Lithobius sp.	Caves along the underground flow of the river Reka-Timavo (Wolf 1938 (loc. as RekaHohlen)), Mala jama pri Veliki groblji ((Matic and Dărăbanţu 1968 (as *L. burzenlandicus wardaranus,* re-examined in this study)), Račiška pečina (Polak et al. 2012), Tikina jama (Stepišnik and Ramšak 2006)	Brezno na Grmadi (11.3.2007, leg. SP), Čendova jama (3.6.2009, leg. MZ, SiP), Česnovka (14.6.2020, leg. AK, JS), Cikova jama (26.3.2007, leg. SP), Gabrovška jama (17.9.2009, leg. SP, VS; 8.9.2009, leg. SP), Jakobova luknja (2.9.2020, leg. AK), Jama jugozahodno od Mašuna (29.9.2002, leg. SP), Jama na Opalah (24.7.2020, leg. PP, EP), Jama na Pucovem Kuclu (25.7.2020, leg. MaP, PP, EP), Jama pod Gavgami (3.6.2022, leg. AK, MZ, entrance part), Jama pod Krogom (6.6.2021, leg. AK, entrance part), Jama pod Smoganico (16.9.2020, leg. AK, entrance part), Jama v doktorjevi ogradi (25.11.2021, leg. MZ, CF, ŠB, EP), Jama v Sodolih (2.7.2020, leg. AK, JS), Jerinovec (21.6.2020, leg. AK, JS, entrance part; 20.4.2022, leg. BR, AL; 4.5.2022, leg. AK, EP, BR, TT, AL, deeper part; 6.10.2022, leg. AK, BR, deeper part), Kamrica jama (5.1.2021, leg. TD), Koševlevka (21.6.2020, leg. AK, JS, entrance part; 10.12.2021, leg. TD, CF, deeper part; 7.1.2022, leg. Unk, entrance part; 30.3.2022, leg. AK, MZ, TD, entrance and deeper part; 5.4.2022, leg. BR, GB, entrance and deeper part; 20.4.2022, leg. AK, CF, deeper part; 4.5.2022, BR, TT, AL, entrance part; 19.7.2022, leg. AK, GB, entrance part; 26.7.2022, leg. TD, AP, deeper part; 9.8.2022, leg. EP, CF, entrance part; 13.10.2022, leg. MZ, ŠB, SM, AP, GB, deeper part; 20.10.2022, leg. MZ, BR, EP, entrance part; 10.11.2022, leg. VZ, HR, MZ, entrance and deeper part), Mačkovica (20.10.2022, leg. AK, entrance part; May 1970, leg. Unk*; 27.12.1969, leg. Unk*; 25.7.1969, leg. Unk*), Mali Obrh spring (12.10.2022, leg. SP), Mivči kevderc (16.9.2009, leg. SP, VS), Mrzla jama pri Ložu (16.7.2007, leg. SP), Otoška jama (12.9.2003, leg. LR, deeper part; 3.10.2003, leg. LR, entrance part; 29.12.2003, leg. LR, deeper part; 16.1.2004, leg. LR, entrance part; 19.3.2004, leg. LR, deeper part; 23.7.2004, leg. LR, entrance part; 13.8.2004, leg. LR, deeper part; 3.9.2004, leg. LR, entrance and deeper part; 24.9.2004 leg. LR, deeper part), Pajkova Reža (27.10.2014, leg. ŠB), Paščipajkovka (2.7.2022, leg. AK, entrance part), Pečina v Borštu (4.9.2022, leg. AK), Pistišekova povšna (20.11.2003, leg. Aka), Planinska jama (4.4.2006, leg. SP; 20.10.2010, leg. MV, TD, MK, JJ), Postojnska jama (12.9.2003, leg. LR, deeper part; 14.11.2003, leg. LR, deeper part; 29.12.2003, leg. LR, deeper part; 6.2.2004, leg. LR, entrance and deeper part; 21.5.2004, leg. LR, entrance and deeper part; 23.7.2004, leg. LR, entrance part; 13.8.2004, leg. LR, entrance part; 3.9.2004, leg. LR, entrance part; 24.9.2004 leg. LR, entrance and deeper part; 14.12.2016, leg. PK, MB, entrance part), Praprotno (3.5.2007, leg. SP), Predjamski jamski sistem (2.9.2020, leg. PK, entrance part; 2.12.2020, leg. PK, entrance part; 19.5.2022, leg. PK, KK, deeper part), Prva nižinska (25.11.2020, leg. TD, ŠB), Raja peč (29.7.2009, leg. MZ), Risova jama (26.6.2022, leg. AK, JS), Slugova jama (11.4.2007, leg. SP), Strmška jama (20.10.2009, leg. SP), Svinjska jama pri Dolenji vasi (23.1.2017, leg. MZ, FK), Škocjanske jame (26.9.2018, PK, entrance part), Tkavčja jama (1.9.2022, leg. AK), Tomažinov brezen (14.6.2020, leg. AK, JS), Trpinova jama (22.5.2022, leg. AK), Vančeva jama (5.11.2004, leg. MZ, MS, LR), Vodovodna jama (15.9.2020, leg. AK, entrance part; 26.7.2010, leg. MZ), Zadlaška jama (21.7.2010, leg. MZ)

Taxon name	Literature findings	New findings
Lithobius stygius Latzel, 1880	Carniola (Attems 1959), Jama 1 v Mahovniku (Matic and Dărăbanţu 1968), Jama pod Smoganico (Verhoeff 1929; Manfredi 1932b; Wolf 1938), Lukova jama pri Zdihovem (Matic and Dărăbanţu 1968), Mačkovica (Verhoeff 1929; Wolf 1938 (as Mackovo jama)), Magdalena jama (Wolf 1938), Mrzla jama pri Ložu (Polak and Pipan 2021), Planinska jama (Latzel 1880; Attems 1929; Wolf 1938; Matic and Dărăbanţu 1968; Matic and Stentzer 1977; Matic 1979; Zapparoli 1989), Podpeška jama (Matic and Dărăbanţu 1968 (as *L. stygius* and *L. jugoslavicus*)), Postojnska jama (Latzel 1880; Attems 1929; Manfredi 1932b; Wolf 1938; Matic 1978), Predjamski jamski sistem (Wolf 1938 (loc. as FurstWindischgratzerhohle), Tekavčja jama (Matic and Dărăbanţu 1968), Velika Karlovica (Matic and Dărăbanţu 1968), Vodna jama (Matic and Dărăbanţu 1968), Zadlaška jama (Verhoeff 1929; Manfredi 1932b; Wolf 1938 (all references loc. as Dantegrotte)), Željnske jame (Matic and Dărăbanţu 1968)	Apolonova jama (17.5.2020, leg. AK, JS, entrance part), Brezno pod Jelen brdom (28.6.2003, leg. FK*), Brezno pri Pojetovih lazih 2 (2.7.2020, leg. AK, JS, entrance part), Črna jama (16.8.2020, leg. PG), Dolga jama pri Koblarjih (20.4.2012, leg. TD; 23.11.2004, leg. MZ, LR, US), Doljna vodena jama (19.5.2020, leg. AK, JS), Drežniška jama (28.2.2016, leg. TD), Fosilni rov 1 (25.7.2021, leg. AK, entrance part), Fučkovski zdenec (23.7.2015, leg. ŽF), Gornja vodena jama (19.5.2020, leg. AK, JS), Jama 1 pri Planinski jami (29.10.2022, leg. MZ, AK, entrance and deeper part), Jama 1 v Mahovniku (24.1.20211, leg. AK, JS), Jama na vzhodnem pobočju Roga (16.5.2020, leg. AK), Jama pod cesto (22.12.2010, leg. Unk), Jama Sv. Loja (17.5.2011, leg. TD), Jama Treh bratov (27.6.2021, leg. AK, entrance part), Jama v kamnolomu (6.9.2005, leg. SP; 27.7.2015, leg. ŽF; 24.8.2006, leg. PT, VZ), Jama v Suhi Rebri (19.4.2020, leg. MZ, ŠB, TD), Jama v Taborski steni (24.9.2003, leg. SP), Jama zahodno od Škrilj (5.4.2020, leg. IK, AK, entrance part), Jelovička jama (21.7.2014, leg. TD), Kobilna jama (2.12.2017, leg. EP), Lobašgrote (24.7.2014, leg. TD; 20.9.2004, leg. PT; 22.9.2020, leg. AK, MR, entrance and deeper part), Lukova jama pri Zdihovem (20.11.2003, leg. BS, SP, DC), Mala Skednenca (26.7.1994, leg. SP*), Mali džot (5.4.2007, leg. SP), Mali Obrh spring (12.10.2022, leg. SP), Mrzla jama pri Ložu (13.10.2022, leg. HR, SM; 16.7.2007, leg. SP), Otoška jama (12.9.2003, leg. LR, deeper part; 24.10.2003, leg. LR, deeper part; 8.12.2003, leg. LR, deeper part; 29.12.2003, leg. LR, deeper part; 16.1.2004, leg. LR, entrance part; 6.2.2004, leg. LR, deeper part; 27.2.2004, leg. LR, deeper part; 19.3.2004, leg. LR, deeper part; 30.4.2004, leg. LR, deeper part; 21.5.2004, leg. LR, entrance and deeper part; 11.6.2004, leg. LR, deeper part; 13.8.2004, leg. LR, deeper part; 3.9.2004, leg. LR, deeper part), Paščipajkovka (2.7.2022, leg. AK, entrance part), Pikčeva jama (13.4.2020, leg. IK, AK; 31.10.1993, leg. IK*), Planinska jama (29.10.2022, leg. MZ, JB, AK, LK, deeper part; 24.11.2009, leg. MK, JJ, AM; 27.4.2020, leg. MZ; 24.4.1986, leg. FP*), Podpeška jama (15.1.2018, leg. IK, ŽK; 24.1.1989, leg. FP*), Postojnska jama (12.9.2003, leg. LR, entrance and deeper part; 3.10.2003, leg. LR, entrance and deeper part; 24.10.2003, leg. LR, entrance and deeper part; 14.11.2003, leg. LR, entrance part; 8.12.2003, leg. LR, entrance and deeper part; 16.1.2004, leg. LR, entrance and deeper part; 27.2.2004, leg. LR, deeper part; 19.3.2004, leg. LR, deeper part; 9.4.2004, leg. LR, entrance part; 30.4.2004, leg. LR, entrance and deeper part; 21.5.2004, leg. LR; 11.6.2004, leg. LR, entrance part; 2.7.2004, leg. LR, entrance and deeper part; 23.7.2004, leg. LR, deeper part; 13.8.2004, leg. LR, entrance part; 3.9.2004, leg. LR, entrance and deeper part; 24.9.2004, leg. LR, entrance part; 14.12.2016, leg. PK, MB, entrance part; 10.2.2022, leg. PK, KK, entrance part; 29.9.2022, leg. PK, PG, entrance part; 20.10.2022, leg. AK, entrance part), Prvoaprilska jama 2 (22.9.2020, leg. AK, MR), Rauhova jama (26.2.2016, leg. TD, EP, DŠ, DK, PeP, NS), Risova jama (26.6.2022, leg. AK, JS), Šepčev skedenj (19.5.2020, leg. AK, JS), Skednevnica (22.5.2022, leg. AK, deeper part), Škratovka (30.9.2016, leg. PT), Snežna jama pri Glažuti (22.9.2020, leg. AK, MR), Strmška jama (20.10.2009, leg. SP), Svinjska jama pri Dolenji vasi (5.1.2011, leg. MZ, KlK, JM, TD), Trpinova jama (22.5.2022, leg. AK), Vančeva jama (23.10.2010, leg. MZ, SiP, TD; 9.5.2010, leg. MZ; 23.11.2004, leg. MZ, US, LR), Velika Karlovica (28.7.1994, leg. SP*), Velika Knežja jama (17.5.2020, leg. AK, JS), Velika Skednenca (28.7.1994, leg. SP*), Veliki kevder v Bukovju (22.5.2022, leg. AK, entrance part), Vetrovna jama pri Laški kukavi (5.12.2013, leg. MZ, PT, TD), Željnske jame (22.9.2022, leg. AK, MR), Zelške jame (8.8.2003, leg. MZ, PT, LL), Zijavka (3.5.2007, leg. SP)
Lithobius tenebrosus Meinert, 1872		Košelevka (13.4.2022, leg. CF, EP, entrance part), Zapostavljena jama (31.7.2020, leg. AK, JS, entrance part)
Lithobius tricuspis Meinert, 1872		Brezno pri Pojetovih lazih 2 (2.7.2020, leg. AK, JS, entrance part), Čendova jama (16.9.2020, leg. AK, entrance part), Ciganska jama pri Predgrižah (22.6.2011, leg. TD, KlK, JM, JJ), Jama med plastmi (20.7.2020, leg. AK, JS, entrance part), Jama na Pucovem Kuclu (25.7.2020, leg. MaP, PP, EP), Jama nad izvirom pri Šinkovčevi žagi (12.5.2009, leg. MZ, SiP), Jama pri Glažuti (22.9.2020, leg. AK, MR), Jama v gradu pri Osojnici (21.7.2020, leg. EvP, PP, EP, TT), Jelenska zijalka (5.8.2022, leg. TD, AZ), Jerinovec (21.6.2020, leg. AK, JS, entrance part), Košelevka (21.6.2020, leg. AK, JS, entrance part; 13.4.2022, leg. CF, EP, entrance part; 12.7.2022, leg. AP, MZ, Dku, entrance part; 19.7.2022, leg. AK, GB, entrance part), Pilanca (19.7.2016, leg. ŽF), Polharjev kevderc (1.9.2020, leg. AK, JS), Predjamski jamski sistem (18.6.2020, leg. PK, deeper part; 2.9.2020, leg. AK; 2.9.2020, leg. PK, entrance and deeper part; 2.12.2020, leg. PK, entrance and deeper part; 27.1.2021, leg. PK, deeper part; 18.11.2021, leg. PK, PG, deeper part; 10.2.2022, leg. PK, KK, entrance and deeper part; 19.5.2022, leg. PK, KK, deeper part; 7.7.2022, leg. PK, deeper part; 29.9.2022, leg. PK, PG, deeper part), Raja peč (29.7.2009, leg. MZ), Ravensko brezno (22.7.2009, leg. MZ, PT), Ruščeva jama (1.6.2009, leg. MZ, PT), Spodmol v Brezovcu (22.8.2003, leg. SP), Zelške jame (19.6.2022, leg. AK, entrance part)

Taxon name	Literature findings	New findings
Lithobius validus Meinert, 1872	Caves along the underground flow of the river Reka-Timavo (Wolf 1938 (loc. as RekaHohlen)), Huda luknja pri Radljah (Matic and Stentzer 1977 (as *Lithobius p. punctulatus*)), Kačna jama (Kos 1987), Mačkovica (Matic 1979 (as *L. punctulatus*)), Škocjanske jame (Matic and Dărăbanţu 1968; Polak 2017)	Jama 1 v Kanjaducah (5.9.2013, leg. TD, FG; 13.5.2015, leg. TD; 11.12.2005, leg. PT), Kačna jama (25.9.2013, leg. TD, FG), Koševelka (21.6.2020, leg. AK, JS, entrance part; 13.4.2022, leg. CF, EP, entrance part), Okno jama (19.7.2021, leg. EP), Predjamski jamski sistem (3.12.2019, leg. PK, deeper part; 18.6.2020, leg. PK, deeper part; 2.9.2020, leg. AK; 2.9.2020, leg. PK, entrance and deeper part; 2.12.2020, leg. PK, entrance and deeper part; 27.1.2021, leg. PK, entrance part; 8.7.2021, leg. PK, PG, entrance part; 18.11.2021, leg. PK, PG, entrance and deeper part; 7.7.2022, leg. PK, entrance and deeper part; 29.9.2022, leg. PK, PG, entrance and deeper part), Škocjanske jame (4.10.2017, leg. PK, entrance part; 6.12.2017, leg. PK, entrance part), Tomažinov brezen (14.6.2020, leg. AK, JS, entrance part), Trpinova jama (22.5.2022, leg. AK)
Lithobius zveri (Matic & Stenzer, 1977)	Planinska jama (Matic and Stentzer 1977), Slovenia, in caves (Stojanović et al. 2021)	

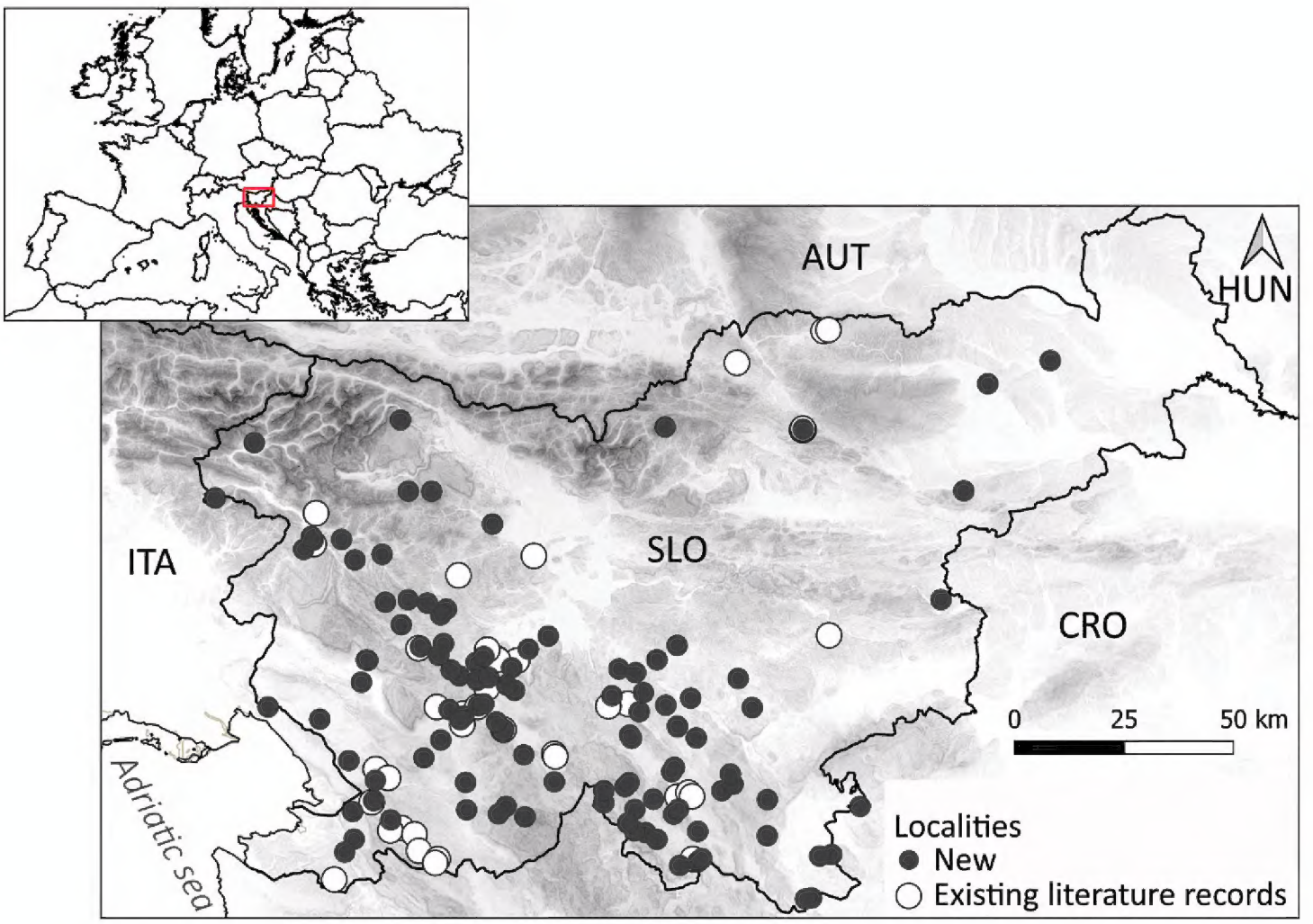

Figure 1. Localities with records of lithobiomorph species in Slovenia. The black dots represent localities, from which lithobiomorph centipedes are reported for the first time, while the white circles represent existing literature records.

Compiled data show that *Lithobius stygius* is the most commonly found species and was reported in 60 sites, presenting almost a third of all reported findings. Species *L. tricuspis*, *L. nodulipes* and *Eupolybothrus tridentinus* were also very common (Figs 2, 3), reported in more than 15 locations. On the other hand, eight species are reported only from a single locality, namely *Lithobius castaneus*, *L. austriacus*, *L. borealis*, *L. latro*, *L. lucifugus*, *L. melanops*, *L. dentatus* and *L. zveri* (Table 1).

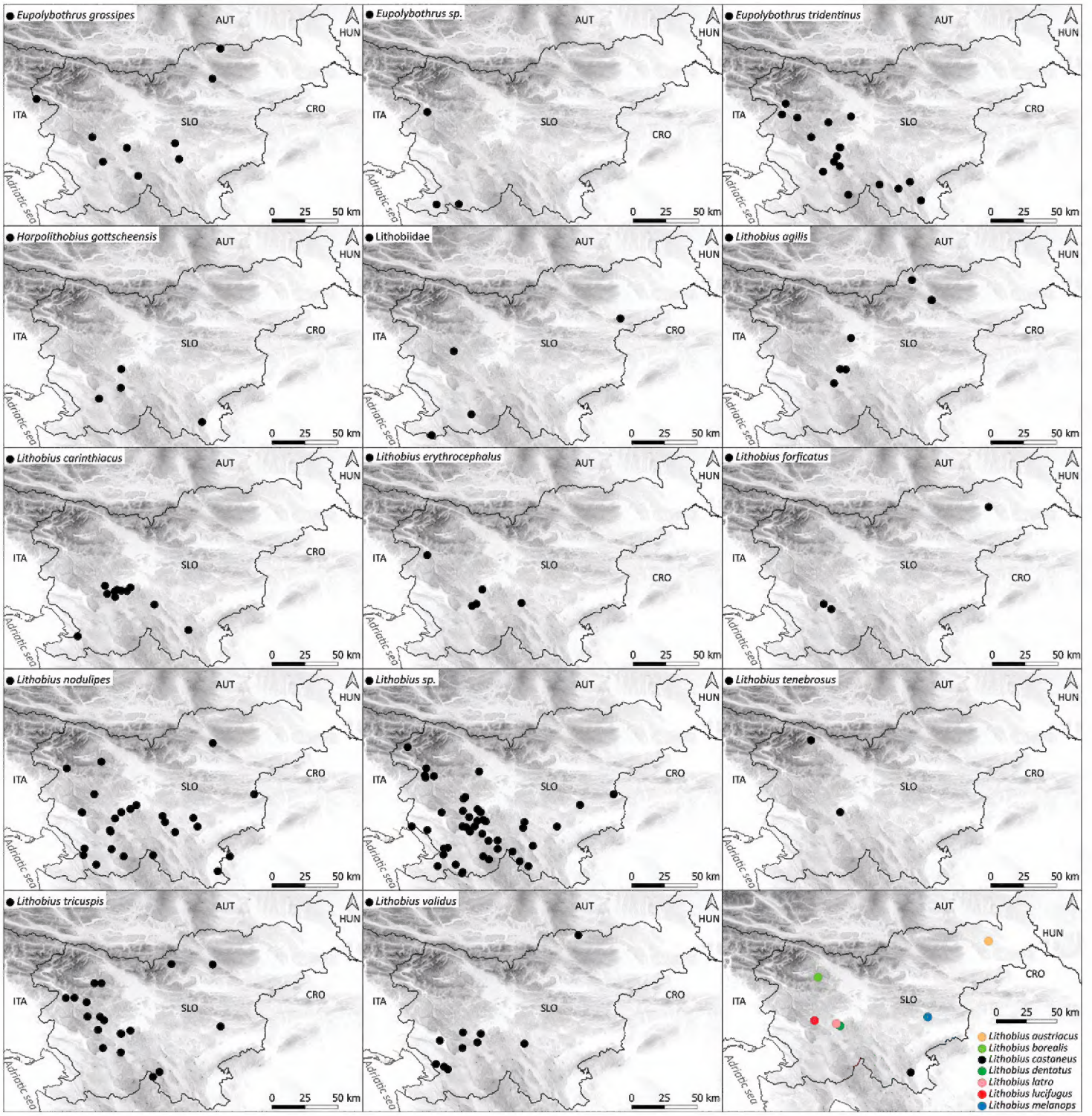

Figure 2. Recorded localities of the surface lithobiomorph centipede species from Slovenian caves.

Discussion

Three lithobiomorph centipede genera, comprising at least 21 species can be found in caves of Slovenia. In addition, almost half of the lithobiomorph species found in Slovenia (Kos 1992a; Stoev 1997) were found in caves at least once. Systematic collecting contributed to a significant increase in the knowledge on centipedes from caves, as 78% the of presented findings are new. Nine species, all of them considered surface and occurring in caves only accidentally, are reported for the first time from Slovenian caves; *Harpolithobius gottscheensis*, *Lithobius austriacus*, *L. borealis*, *L. castaneus*, *L. carinthiacus*, *L. dentatus*, *L. nodulipes*, *L. tenebrosus* and *L. tricuspis*.

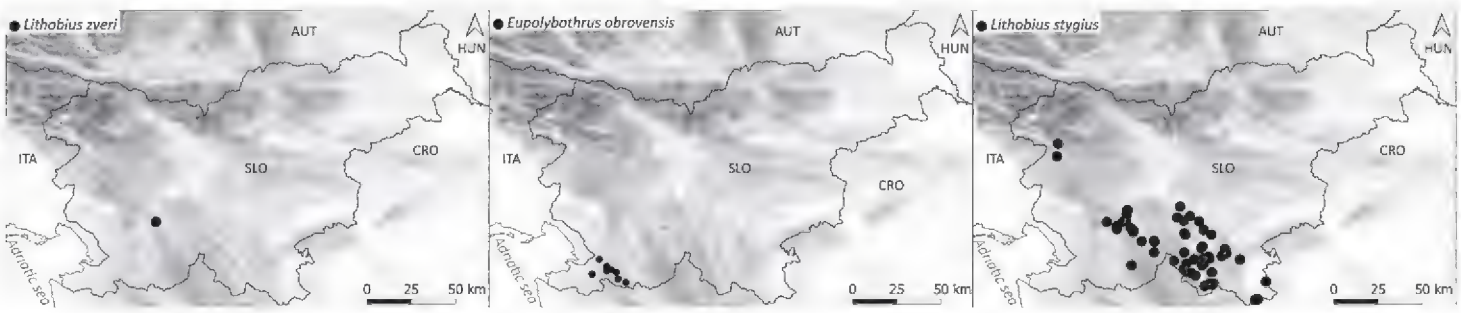

Figure 3. Recorded localities of the troglobiont lithobiomorph centipede species from Slovenian caves.

Records of many centipede species from caves opens a series of questions on the differences of their habitat preferences towards subterranean habitats. Most of the recorded specimens from our dataset belong to surface species, but it is unclear whether these species occur in caves only accidentally, occasionally, or caves present a regular part of their habitat. Some species were found only in a few caves, indicating their accidental occurrence there, similar to what was found in proturans (Galli et al. 2021). On the other hand, some species were frequently found in caves, which may indicate their active use. Different preferences towards caves between species are partly supported also by other studies, e.g., genus *Eupolybothrus* is known to have many species occurring often or solely in caves (Stoev et al. 2010; Akkari et al. 2017). The species *E. obrovensis*, *L. stygius* and *L. zveri* have so far not been found outside caves and are thus considered troglobiotic (Sket 2008; Ozimec and Komerički 2009; Zagmajster et al. 2021). On the other hand, strict delimitation between caves and surface habitats is not unambiguous. The turnover is gradual and continuous, and includes many cracks and fissures in the epikarst (Culver and Pipan 2008, 2014) – a transition zone between surface and deeper subterranean habitats (Prous et al. 2004; Kozel et al. 2019). Finally, the caves present only a sampling point that is directly accessible to humans. In several cases, the specimens were found in the entrance parts of caves, where environmental conditions are similar in many aspects to those in the upper soil layers (e.g., high availability of organic matter and high humidity) which are primary habitat for centipedes and other edaphic organisms (Voigtländer 2011). The connectivity of those habitats is indicated also by our results, as many surface centipedes were recorded despite the assumption that caves are not their main habitat. Therefore, their findings likely also reflect the ecological conditions around the caves and their geographic position. One interesting example is the finding of the species *L. austriacus* in an artificial tunnel in Osek in Northeast Slovenia. This species is known only from mostly non-karstic Northeastern part of Slovenia and countries to the East and North (Simaiakis and Strona 2015). On the other hand, species *L. borealis* is generally found in higher altitudes, as was also the case in our finding.. Interestingly, species *E. tridentinus*, *L. nodulipes*, *L. stygius and L. tricuspis* were found in caves which are located in an altitudinal span of approximately 1000 m a.s.l. This might not be surprising as those were the most commonly recorded species.

Taxonomic comments

The compilation of occurrence dataset inevitably relates to the current knowledge on lithobiomorph centipede taxonomy, which is incomplete, prone to temporal changes, and additionally complicated by varying taxonomic interpretations between the researchers as several taxa need revision (Zapparoli 2003; Bonato et al. 2011). Due to mentioned shortcomings the comparison of literature records is challenging and, the taxonomical curation of the dataset was necessary to include currently valid names and to address possible misidentifications originating from different taxonomic concept. As example, some specimens cited in Matic and Dărăbanţu, (1968) where re-examination of material was possible, were assigned to different species; reported finding of *E. fasciatus* and *L. microps*, correspond to *E. grossipes* and *L. carinthiacus*, respectively. Determinations of specimens reported as *L. burzenlandicus wardaranus* could not be conclusive due to damaged material, but the finding from Mala jama pri Veliki Groblji corresponds to a yet undescribed taxon *Lithobius anici* nomen nudum, reported from several surface sites in Slovenia (Kos 1995; Kuralt et al. 2022). Similarly, the finding from Vratnica likely belongs to *Lithobius carinthiacus* (due to presence of three spines on ventral side of 15th prefemur), but specimen is too damaged to make conclusive determination. Furthermore, findings of *Eupolybothrus leostygis*, reported by some authors, were corrected to *E. obrovensis* as suggested by Verhoeff (1934) and Eason (1983). Interpretation of taxonomic status for *Lithobius microporus* Verhoeff, 1937, *Lithobius jugoslavicus* Matic & Dărăbanţu, 1968 and *Lithobius glabratus fuscus* Folkmanova, 1946 is treated as dubious. They are considered as probable synonyms of *Lithobius lucifugus* L. Koch, 1862, *Lithobius stygius* Latzel, 1880 and *Lithobius melanops* Newport, 1845 respectively (Stoev 2001; Bonato et al. 2016); however, their identity was not thoroughly studied. Similarly, synonymy of *L. illyricus* Latzel, 1880 with *L. erythrocephalus* C.L. Koch, 1847 is stated in ChiloBase 2.0, however it was never formally established and the species is considered valid by some authors (Kos 1992a; Stoev 1997; Stagl and Zapparoli 2006). On the other hand, Zapparoli (1989), who reported *L. erythrocephalus* from caves in Slovenia, considered that characters of *L. illyricus* are within the variation of *L. erythrocephalus*. Existence of potential new species, some of which might represent morphologically identical, cryptic species, additionally hinders complete overview of the species diversity. Their potential presence was detected among the examined individuals in our study and was also reported in literature (Zagmajster et al. 2021). This is expected as there have been descriptions of new species from the Dinaric caves in recent time (Stoev et al. 2015; Akkari et al. 2017; Stojanović et al. 2021) and cryptic diversity is a common problem in many centipede groups (Spelda et al. 2011; Del Latte et al. 2015; Kuralt et al. 2022; Peretti et al. 2022).

Taxonomic knowledge of several lithobiomorph species that were described from Slovenian caves changed over time. Eyeless centipede, *Eupolybothrus obrovensis* (Fig. 4) was described based on subadult male under the name *Lithobius obrovensis*. Species type locality is "Höhle von Obrovo" (Verhoeff 1930), interpreted as Dimnice cave by most of the subsequent authors (Matic and Dărăbanţu 1968; Ozimec and Komerički

Figure 4. Three lithobiomorph centipede species found in Slovenian caves. Subterranean centipede *Lithobius stygius* (upper left), surface species *Lithobius nodulipes* (upper right) and subterranean species *Eupolybothrus obrovensis* (bottom) (Photo: Teo Delić).

2009) or as Pečina v Borštu (Wolf 1938; this article). Later work by Verhoeff (1933) provides information on an adult male from Medvedjak and Matic & Daranbatu (1968) provided a description of a female from Dimnice. Nevertheless, a redescription of the species, based on the adult male and the consolidation of the type locality is needed. Attems (1908, 1929) found the species even before it was formally described in 1930, proclaiming it for *Eupolybothrus leostygis*, species which is otherwise narrowly distributed in Southern Croatia and Bosnia and Herzegovina. This error is mentioned already by Verhoeff (1934), however, several other authors (Manfredi 1932b; Wolf 1938) cited this finding, and species *E. leostygis* ended up even in the checklist of centipedes in Slovenia (Kos 1992a). In addition, the locality name Medvedova jama (referring to cave Medvedjak, Cad. nr. 881, "bear cave") was translated into Italian "Grotta dell'Orso" and misinterpreted as a cave near Gabrovizza, San Primo in Italy (Manfredi 1932a, 1932b; Wolf 1938; Eason 1983). *Eupolybothrus obrovensis* was long known only from few caves, but the speleobiological surveys after the year 2000 yielded more findings, improving our knowledge on the species's narrow distribution. The species occurs in Primorska and Istria regions in Slovenia and Croatia (Table 1; Ozimec and Komerički 2009). The species is listed as Vulnerable on the Slovenian and Croatian Red List (Kos 1992b; Wraber et al. 2002; Ozimec and Komerički 2009) and is protected species by the Croatian national legislation (Official Gazette of the Repub-

lic of Croatia No. 70/05, 139/08). Presumably, the species is vulnerable to changes in habitat and cave fauna, especially due to its narrow distribution and high position in the food chain (Ozimec and Komerički 2009).

Species with the highest number of occurrences, *Lithobius stygius* (Fig. 4), was described from Postojnska jama by Latzel (1880) and reported in caves through the Balkans (Stoev 2001). The existing reports are subjected to some taxonomical unclarities, emphasising the need for its further study. Examples from the area of Slovenia include reported species *L. erythrocephalus* and *L. illyricus*, surface species similar to *L. stygius*, from several caves (Attems 1929; Matic and Dărăbanţu 1968; Zapparoli 1989; Gasparo 1995, 1998). It is unclear whether all of them are truly correct identifications or possible misidentifications, and refer to findings of *L. stygius* or another, similar, and potentially new species. On the other hand, species *Lithobius jugoslavicus* Matic & Dărăbanţu, 1968 is one of the possible junior synonyms of *L. stygius*, where revision is needed to clarify its status (Stoev 2001). It is very likely that the species was described based on an abnormal individual. In some of the works it was referred also as *Lithobius corneliae* Stoev, 1997 in attempt to distinguish it from *Lithobius jugoslavicus* (Hoffer, 1937) (now a synonym of *Lithobius matulici* Verhoeff, 1899, occurring in Bosnia and Herzegovina) (Stoev 1997; Dányi et al. 2019). Preliminary genetic analyses covering the North-western Dinarides showed that the species *L. stygius* is occurring in the south-eastern part of Slovenia and north-western Croatia, while there exists also morphologically similar, but genetically distinct species (Kos A., unpublished). Furthermore, there have been records of synonyms *Lithobius cerberi* Verhoeff, 1943 and *Oligobothrus luciani* Folkmanová, 1935 in the Balkans (Folkmanova 1935; Verhoeff 1943; Eason 1983; Stoev 2001), as well as possible synonym *L. temnensis* Verhoeff, 1943, which was reported from caves as well as surface (Zapparoli 2002).

Lithobius zveri is eyeless centipede and was described by Matic and Stenzer (1977). Even though it was found in one of the most surveyed caves, Planinska jama, it is known only from a single specimen. This might be due to its rarity, our inability to sample its main habitat, small size or lack of targeted sampling. The species is morphologically well separated from other species (Stojanović et al. 2021), however further findings on this elusive and presumably highly endemic species are needed to better understand its taxonomic position.

Polybothrus cerberus Verhoeff, 1929, *Lithobius microporus* Verhoeff, 1937 and *Lithobius glabratus fuscus* Folkmanova, 1946 were also described from Slovenian caves, but are now considered as synonyms of *Eupolybothrus tridentinus* (Fanzago, 1874), *Lithobius lucifugus* L. Koch, 1862 and *Lithobius melanops* Newport, 1845, respectively (Eason 1983; Zapparoli 1989; Stoev 1997). To make it even more complicated the identity of the type locality for the subspecies *Lithobius glabratus fuscus*, described as Lok. 776 Vranja peć, is unclear. Stoev (1997) suggested that the locality might be in Croatia. Naming of the localities follows the collection Biospeleologica balcanica, enabling a direct comparison with other literature. Willmann (1941) describes this locality as Vranja peć bei Saxenstein, Carniola. Based on an examination of old names for toponyms and settlements in Slovenia and Croatia, we concluded that this cave is most likely Raja peč (Cad. nr. 371, one of its synonyms is Vranja pečina) near town

Boštanj, which was referred to as Savenstein in German (the name was apparently misspelt by researchers).

Open challenges

Occurrence and distribution of lithobiomorph centipedes in Slovenia open many interesting questions and directions for further studies. The frequent findings of different surface centipede species underground open question on the connectivity of subterranean and surface habitats. It remains open to investigate, how the species composition in caves is related to the overall centipede species diversity in the region. Further on, lithobiomorph centipedes may present an interesting group to study processes related to colonization of subterranean habitats, especially as there are groups of species that can be found in the surface-subterranean ecotone as well as deep in caves.

As top predators and K-strategists (Albert 1983; Vahtera et al. 2020), lithobiomorph centipedes might have an specific position in subterranean ecosystems, however, their role in communities is still understudied. Different surface species might be part of different communities and are presumably more interconnected with community at cave entrances, while exclusively subterranean species are likely part of the communities deeper in caves (Novak et al. 2012; Cuff et al. 2021). In the Dinarides, there are several centipede species that were found in deep parts of caves, with geophilid centipede *Geophilus hadesi* Stoev, Akkari, Komerički, Edgecombe & Bonato, 2015 holding depth record with finding in cave Lukina jama – Trojama cave system, at depth 1100 m (Stoev et al. 2015). Given the lack of ecological data, further studies would be needed to investigate the ecology of centipedes and their role in subterranean communities.

This paper represents an important contribution to the knowledge of diversity of centipedes in the caves of Slovenia. It is clear that centipedes are a diverse group of animals that, despite the rich history of research require further faunistic and ecological studies to gain at least a basic understanding of their role in communities within subterranean realm. With the data at hand, the understanding of their taxonomy is also far from complete, as is evident from the existence of numerous taxonomic issues. Therefore, further work should aim to resolve taxonomic status, include molecular information on the specimens to improve the resolution of centipede species diversity and their phylogenetic relationships, and to set a solid framework for future ecological studies.

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Supplementary material 1

Detailed information on localities with reported lithobiomorph centipedes

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Data type: table (.xlsx file)

Explanation note: Locality name is provided, followed by the National Cave Registry number, closest and largest settlement, latitude and longitude, altitude (rounded to 10 m), number of recorded taxa and number of taxa with first report on the occurrence from the cave (number of taxa was determined as minimal number, counting only lowest determined categories in case of e.g. both species and genus level determinations), information whether this work is reporting on lithobiomorph centipedes from the locality for the first time and additional comments (e.g. synonyms reported in the cited resources).

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